# BIONOMICS OF *TRYPOXYLON (TRYPARGILUM) ANTROPOVI* AND *TRYPOXYLON (TRYPARGILUM) AESTIVALE* (HYMENOPTERA, SPHECIDAE)

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## ABSTRACT

Nests of the mud-dauber wasps *Trypoxylon (Trypargilum) antropovi* Coville, 1985 (n=14) and *Trypoxylon (Trypargilum) aestivale* Richards, 1934 (n=9) were collected from walls of abandoned houses. Nests were made of mud, and their form was characterized by vertical, side by side tubes open at the bottom and the tubes consisted of a linear series of brood cells separated by mud partitions and plugged at the end with mud. Brood cells of *T. antropovi* were provisioned with spiders of the family Araneidae. Females of the two species were larger than males, whereas females and males of *T. antropovi* were larger than *T. aestivale*. Natural enemies included Chrysididae and *Melittobia* for both species, Chalcididae and Ichneumonidae for *T. antropovi* and *Anthrax* for *T. aestivale*.

KEYWORDS. Sphecidae, *Trypoxylon*, wasps, nest, natural enemies.

## INTRODUCTION

The genus *Trypoxylon* is divided into the subgenera *Trypoxylon* and *Trypargilum*, (Richards, 1934). Species of *Trypargilum* are restricted to the Western Hemisphere, occurring from Canada to Argentina, with most of them being restricted to the Neotropical region. Species of this subgenus are distributed into the *albitarse* (*albitarse, fuscipenne* and *poultoni* complex), *nitidum* (*aureovestitum, excavatum, fugax, nitidum, punctulatum, spinosum* and *vagum* complex) and *superbum* groups (Bohart & Menke, 1976; Coville, 1982).

The species of the *albitarse* group construct mud nests on sheltered vertical surfaces such as walls, under bridges and other man-made structures in addition to cliff faces and tree trunks. The nests usually consist from 1 to 6 vertical tubes of mud set side by side and

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open on the bottom end. Normally the wasps first construct an exposed mud tube and then begin to provision the cell at the upper end (RAU, 1928; CROSS **et al.**, 1975). Three to six cells are constructed in sequence per tube, and provisioned with paralyzed spiders. The egg is laid on the abdomen of one of the last spiders stored, and a mud partition is placed to seal the cell. After all cells are completed, the female seals the tube entrance with a thicker plug of mud (BOHART & MENKE, 1976; COVILLE, 1982).

The species show interesting differences, which may provide clues to the probable origins and selective pressures acting to maintain paternal behavior (HOOK & MATTHEWS, 1980). For this reason detailed comparative studies on these species are particularly valuable, especially with respect to the poorly understood tropical species (BROCKMANN, 1992).

The purpose is to present biological data on *Trypoxylon (Trypargilum) antropovi* Coville, 1985 and *Trypoxylon (Trypargilum) aestivale* Richards, 1934 belonging to the *albitarse* group. The first, included in the *albitarse* complex, described from nests obtained in Mexico, whereas the other is included in the *fuscipenne* complex which occurs from Mexico to Brazil (COVILLE, 1982).

## MATERIAL AND METHODS

Study areas: 1, Fazenda Santa Carlota, Cajuru (=Ca), SP (21°17'-18' S, 47°12'-18' W). The vegetation consists of semideciduous mesophyll and riparian forests, "cerrado" (s.l.), "cerradão" and various types of plantations, with altitudes ranging from 540 to 944 m; 2, Estação Experimental de Zootecnia de Sertãozinho (=Se), SP (21°8' S, 47°59' W), is characterized by semideciduous mesophill forests and pastures, with a mean altitude of 548 m; 3, Fazenda Cascata, Santa Rita do Passa Quatro (=SR), SP (21°42' S, 47°28 W) is characterized by orange groves and other plantations, with a mean altitude of 759 m; 4, Base de Estudos de Ecologia e Educação Ambiental da Serra do Japi, Jundiaí (=Ju), SP (23°11' S, 46°52' W). The vegetation consists of semideciduous mesophyll forests, with altitudes ranging from 700 to 1300 m. In these regions two distinct seasons are recognized: cold, dry season (May to August) and hot, wet season (September to April). In relation to altitude, yearly low mean temperatures ranging from 15.7°C to 19.2°C were observed in Jundiaí.

The nests were collected using a palette knife and taken to the laboratory. All nests were opened to analyze their contents and structures. Cocoons were placed in individual vials labeled with the nest and cell number and kept at room temperature. The nests containing larvae were placed in plastic boxes to allow for their development until the period of spinning cocoons. The prey from cells in which the immatures did not develop were collected and preserved in 80% ethanol for later identification. The emerged adults were captured, killed with ethyl acetate, and labeled.

Because the nests of *T. aestivale* had been constructed on a substrate with a rough surface, they were not collected, and some measurements were not carried out. These nests were opened in their places of origin, and immatures and prey were collected from them, placed in individual vials, labeled and taken to the laboratory.

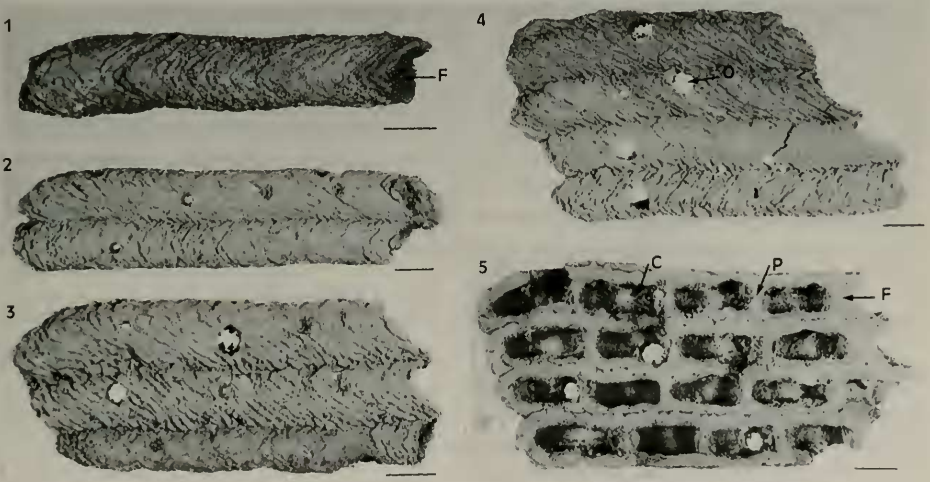
The greatest width of the head (GWH) and the length of the marginal cell of the anterior wing (WL) were used to determine the width of produced individuals. Voucher specimens were deposited in the Departamento de Biologia, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, USP, Ribeirão Preto, SP.

## *Trypoxylon (Trypargilum) antropovi* Coville

*Trypoxylon* sp., near *palliditarsus;* RAU, 1943.
*Trypoxylon (Trypargilum) giganteum;* COVILLE, 1982.
*Trypoxylon (Trypargilum) antropovi* COVILLE, 1985.

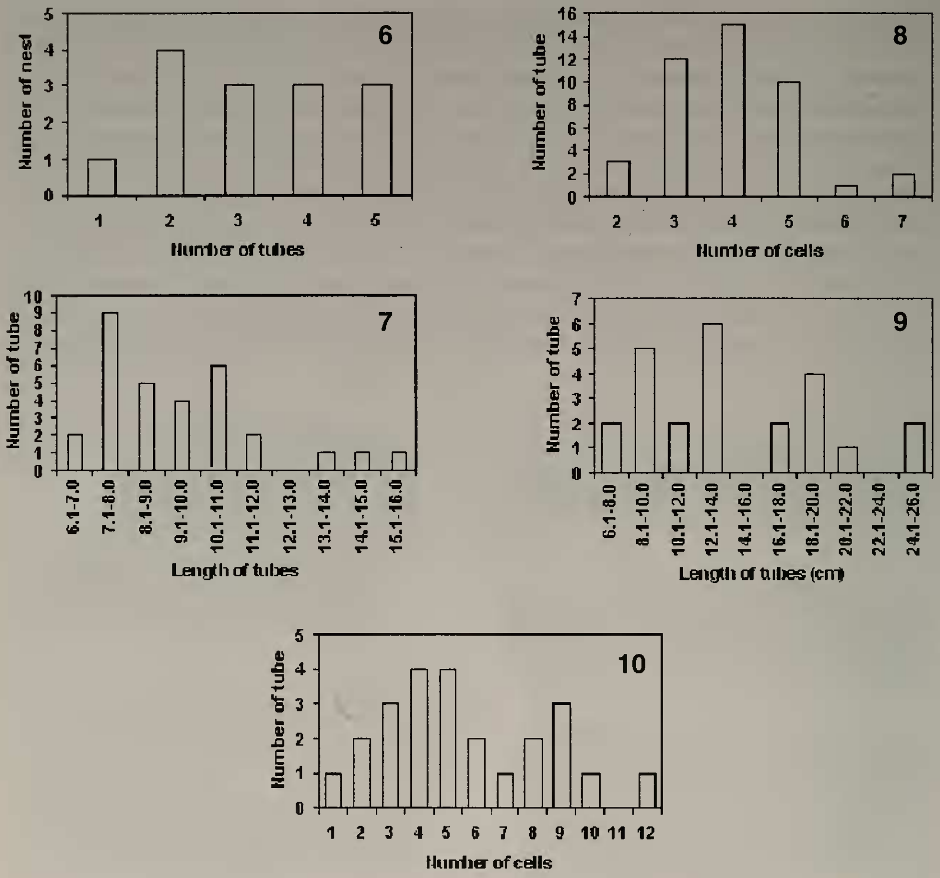
Nest structure and number. A total of 14 nests of *T. antropovi* were obtained: 11 in Ca (2 on May/95, 5 on July/95, 1 on August/95, 2 October/95 and 1 on August/96), 2 in SR (October/95) and 1 in Se (August/95). The nests were constructed with mud of one or more colors, an indication that females may switch mud collection sites during nest construction. The nests were found on the walls of abandoned houses with tubes constructed side by side and open at the bottom (figs. 1-5). The nests consisted from 1 to 5 tubes (x= 3.8 ± 2.4, n= 14) (fig. 6) with "chevron like", inverted V-shaped ribs or ridges. The length of these tubes ranged from 6.7 to 15.3 cm (x= 9.3 ± 2.3 cm, n=32), the highest frequency ranging from 7.1 to 11 cm (fig. 7). At the place of contact with the substrate the external width of the tubes ranged from 10.5 to 13.8 mm (x= 11.7 ± 0.9 mm, n=25), and the thickness of the wall ranged from 1.3 to 3.5 mm (x= 2.7 ± 0.5 mm, n=51); the external height of the tubes ranged from 9.9 to 12 mm (x= 11.2 ± 0.5 mm, n=21).

The cells were constructed in linear series, provisioned with paralyzed spiders and closed with mud partitions. The number of cells per tube ranged from 2 to 7 (x= 4 ± 1.1, n=43), with the greatest frequency ranging from 3 a 5 cells (fig. 8). The total number of cells per nest ranged from 3 to 25 (x= 12.7 ± 6.8, n=14). The length of female cells, ranging from 14.6 to 22.7 mm (x= 18.1 ± 1.5 mm, n=39), was significantly different (Mann-Whitney, Z= 3.97, $p<0.05$) than that of males which ranged from 14.3 to 19.5 mm (x= 15.9 ± 3.5 mm, n=24). The internal width of the cells, at the place of contact with the substrate, ranged from 6.7 to 9 mm (x= 7.9 ± 0.6 mm, n=79). This little variation can be related to the fact that the cells belonging to same tube have similar widths. Vestibular cells were not observed in the nests.



Figs. 1-5. Nests of *Trypoxylon antropovi*: 1, nest with one tube; 2, nest with two tubes; 3, nest with three tubes; 4, nest with four tubes; 5, nest with four tubes in ventral view. C, cell; F, final plug; O, orifice of adult emergence; P, partition. Lines, 1.0 cm.

The two surfaces of a partition differed in their aspect. The top surface (floor of the cell just completed) has roughly the concentric nature of the partition formation. The bottom surface (top of the succeeding cell) is smooth and shows a short, medial nipple-



Figs. 6-10. *Trypoxylon antropovi*: 6, frequency distribution of the number of tubes per nest; 7, frequency distribution of the length of the tubes; 8, frequency distribution of the number of cells per tube. *Trypoxylon aestivale*: 9, frequency distribution of the length of the tubes; 10, distribution frequency of the number of cells per nest.

like or tubercular prominence. The thickness of the cell partitions ranged from 1.4 to 4.4 mm (x= 2.8 ± 0.6 mm, n=61). The tubes begin with the female constructing a mud wall, which is hemispherical, or bluntly acuminate (at the top of the tube). The thickness of these walls ranged from 2.4 to 8.7 mm (x= 5 ± 0.6 mm, n=28). The last cell partition and randomly placed mud balls (producing a rough surface) composed the final plug; they formed an oblique surface that had, medially, a thickness ranging from 3.7 to 22.7 mm (x= 9.9 ± 4.7 mm, n=23) at the place of contact with the substrate.

Cocoons, adults size and sex ratio. The cocoons were brittle, dark brown, more or less shiny, smooth and cylindrical. The anterior end was rounded with a coarse, not shiny crown of sand grains. They were supported within the cell by a loose matrix of silken threads. The cocoons of female (n=8) ranged from 17.2 to 19.2 mm (x= 18.2 ± 0.6 mm) in length and from 6.0 to 6.7 mm (x= 6.2 ± 0.2 mm) in diameter, whereas the cocoons of male (n=3) ranged from 16.4 to 16.6 mm (x= 16.5 ± 0.1 mm) in length and from 5.6 a 5.7 mm (x= 5.6 ± 0.06 mm) in diameter. The cocoons female were larger and wider than the cocoons of male (Mann-Whitney, Z= 2.34 and Z= 2.37, respectively, both p<0.05).

Although there was some overlap in size distribution, the females with the GWH ranging from 3.59 to 4.23 mm and the WL from 3.24 to 3.94 mm (n=25) were significantly larger than males whose GWH ranged from 3.13 to 3.88 mm and WL ranged from 2.78 to 3.59 mm (Mann-Whitney, Z= 5.67 and Z= 5.60, respectively, both p<0.05).

The sex ratio determined for the population produced from the nests (98 cells) was 1.4 females to 1 male which is significantly similar to 1:1 ($X^2$= 2.94, df=1, p>0.05). Emergence holes in peripheral tubes were made in the side or on top. In others tubes, the emergence holes were only on top.

Collected preys, mortality and natural enemies. The number of prey per cell ranged from 4 to 9 (x= 6.4 ± 1.7, n=8). All spider prey (n=36) taken from 6 cells were from the family Araneidae: *Eriophora edax* (Blackwall, 1863) (21 j, 1 m e 1 f), *Parawixia monticola* (Keyserling, 1892) (8 j e 1 f), *Eustala* sp.1 (2 m), *Eustala* sp.2 (1 f) and *Dubiepeira* sp. (1 f).

Out of 179 cells examined, 9 adults had already emerged, 2 were in the process of being provisioned; samples were lost from 5 cells, and adults of other species emerged from 3 cells. Among the remaining cells (n=160) mortality of immatures was observed in 38.1% (egg= 9.8%, larvae= 21.3%, pre-pupae= 16.4%, pupae= 18.8% and parasitoids= 34.4%). The parasitoids were Chalcididae (n= 8), Ichneumonidae (n= 4), Chrysididae (n= 2), *Melittobia* sp. (n= 2) and the rest were not identified (n= 5).

## *Trypoxylon (Trypargilum) aestivale* Richards

*Trypoxylon (Trypargilum) aestivale* Richards, 1934

Nest structure and number. Nine nests were obtained (1 in July 7 in September and 1 in October/95). The nests were structurally similar to that of *T. antropovi*. They had from 2 to 4 tubes (x= 2.78 ± 0.97) with lengths ranging from 6.2 to 25 cm (x= 14 ± 5 cm, n=21) with the most common lengths occurring from 8.1 and 10, 12.1 and 14 and 18.1 and 20 cm (fig. 9). The number of cells per tube ranged from 1 to 12 (x= 5.7 ± 3.12, n=25) with most common being 4 to 5 cells (fig. 10). The total number of cells per nest ranged from 5 to 35 (x= 16 ± 9.5, n=9). Vestibular cells were not observed in the nests.

Cocoons, adults size and sex ratio. The cocoons of *T. aestivale* are similar to that of *T. antropovi*. In length, the female cocoons (n=21) ranged from 14.5 to 17.2 mm (x= 15.8 ± 0.6 mm) and in diameter from 5.2 to 6.1 mm (x= 5.6 ± 0.2 mm). In length, the male cocoons (n=14) ranged from 12.8 a 14.9 mm (x= 14 ± 0.7 mm) and in diameter from 4.5 to 5.4 mm (x= 5.1 ± 0.3 mm). The female cocoons were larger and wider than that of males (Mann-Whitney, Z= 4.76 and Z= 4.09, respectively, both p<0.05).

The females with the GWH ranging from 2.9 to 3.48 mm and WL from 3.07 to 3.77 mm (n=25) were significantly larger than males whose GWH ranged from 2.78 to 3.42 mm with WL ranging from 2.32 to 3.13 mm (Mann-Whitney, Z= 4.44 and Z= 5.57, respectively, both p<0.05). Nevertheless, there was some overlap in size distribution. The sex ratio determined for the population produced from the nests (61 cells) was 1.3

females to 1 male which is significantly similar to 1:1 ($X^2$= 1.05, df=1, $p>0.05$).

Mortality and natural enemies. Out of 144 obtained cells, adults had already emerged from 9 cells, and 3 were being provisioned. Among remaining cells (n=132) immature mortality was observed in 53.8% of the cells (egg= 32.4%, larvae= 12.6%, pre-pupae= 31%, pupae= 14.1% and parasitoids= 9.8%). The parasitoids were Chrysididae (n=3), *Melittobia* sp. (n=2), *Anthrax* sp. (n=1) and one remained unidentified.

## DISCUSSION

*Trypoxylon antropovi* and *T. aestivale* are similar in number of tubes and cells per nest. There are important differences in others attributes. The tubes of *T. aestivale* nests were more delicate and larger than those of *T. antropovi*. Consequently these tubes had more cells. Males and females of *T. antropovi* are larger than *T. aestivale* in GWL and WL. Similarly, the male and female cocoons of the first species were larger than those of the second species with respect to length and diameter (tab. I).

Sex ratio was practically the same for the two species. In general, the immature mortality percentage was greater for *T. aestivale*. The highest mortality rates were observed in the egg and pre-pupae stages. In the other immature stages, and in mortality caused by parasitoids, the rates were greater for *T. antropovi*. In relation to the parasitoids the difference was due to the presence of individuals of the family Chalcididae in nests of *T. antropovi*.

Table I. Comparison of selected biological attributes of *Trypoxylon antropovi* and *Trypoxylon aestivale*. All values are based on range and %. Sample sizes are given in the text. WL, length of marginal cell of the anterior wing; GWH, greatest width of the head.

| Attributes | *T. antropovi* | *T. aestivale* | t test $p<0.05$ |
|---|---|---|---|
| Number of tubes | 1 - 5 | 2 - 4 | |
| Length of tubes | 6.7 - 15.3 | 6.2 - 25.0 | t= 4.65 |
| Number of cells/tube | 1 - 7 | 1 - 12 | t= 3.26 |
| Number of cells/nest | 3 - 25 | 5 - 35 | |
| Male size (mm) (WL) | 2.78 - 3.59 | 2.32 - 3.13 | t= 5.65 |
| Male size (mm) (GWH) | 3.13 - 3.88 | 2.78 - 3.42 | t= 3.53 |
| Female size (mm) (WL) | 3.24 - 3.94 | 3.07 - 3.77 | t= 3.83 |
| Female size (mm) (GWH) | 3.59 - 4.23 | 2.90 - 3.48 | t= 4.54 |
| Sex ratio (% of females) | 59.2% | 57.4% | |
| Length of male cocoons (mm) | 16.4 - 16,6 | 12.8 - 14.9 | t= 6.25 |
| Length of female cocoons (mm) | 17.2 - 19,2 | 14.5 - 17.2 | t= 10.0 |
| Diameter of male cocoons (mm) | 5.6 - 5,7 | 4.5 - 5.4 | t= 2.94 |
| Diameter of female cocoons (mm) | 6.0 - 6,7 | 5.2 - 6.1 | t= 7.22 |
| Mortality of immatures | 38.1% | 53.8% | |
| Egg | 9.8% | 32.4% | |
| Larvae | 21.3% | 12.6% | |
| Pre-pupae | 16.4% | 31.0% | |
| Pupae | 18.0% | 14.1% | |
| Parasitoids | 34.4% | 9.8% | |

The nest architecture of *T. antropovi* and *T. aestivale* is similar to that of other species of the *albitarse* group described by RAU & RAU (1916); RAU (1928, 1943); KROMBEIN, (1967); MATTHEWS & MATTHEWS (1968); CROSS **et al.**, (1975); BARBER & MATTHEWS (1979); COVILLE (1982); BROCKMANN & GRAFEN (1989); BROCKMANN (1980, 1992) and DAWNING (1996). Contrary to that observed in this work, RAU (1943) describes a nest of *T. antropovi* with a coarse exterior that lacks the V-shaped mud ribs or ridges. *T. politum* Say, 1837 nest in hollow bamboo stems lined with mud (BARBER & MATTHEWS, 1979).

According to CROSS **et al.** (1975), females of *T. politum* may construct tubes on top of those in contact with the substrate, forming groups of tubes. In these cases, more than one female may add tubes to the already existing cluster. She may do this at the same time as other females or at a later time.

The length of the brood cells varied among the species, within the same species, and between the sexes of the individuals produced. CROSS **et al.**, (1975); BROCKMANN & GRAFEN (1989) in *T. politum* and BROCKMANN (1992) in *T. monteverdae* Coville, 1982 observed that female cells were larger than male cells. This was observed as well in this study for *T. antropovi*.

The analysis of prey collected by *T. politum* (RAU, 1928, 1944; MUMA & JEFFERS, 1945; LIN, 1969; CROSS, **et al.**, 1975; BARBER & MATTHEWS, 1979; REHNBERG, 1987; BROCKMANN & GRAFEN, 1992), *T. mexicanum* (Saussure, 1867) (RAU, 1943) and *T. monteverdae,* (COVILLE, 1982; BROCKMANN, 1992), showed that 100% were spiders of Araneidae family. MUMA & JEFFERS (1945), however, observed that females of *T. politum* collected 2% of individuals from spiders of the Theridiidae family. They speculated that this was probably due to accidental selections by the female wasp. The analysis of the samples in this study showed the preference for Araneidae, because 100% of prey collected by *T. antropovi* belong to this family. Thus, *T. politum* mostly collected spiders of the following Araneidae genera: *Neoscona* Simon, *Araneus* Clerck and *Eustala* Simon (RAU, 1928; MUMA & JEFFERS, 1945; CROSS **et al.**, 1975; BARBER & MATTHEWS, 1979; REHNBERG, 1987). These are different from the most common genera collected by *T. antropovi*. The preference for juvenile prey observed in *T. politum* (88%) (BARBER & MATTHEWS, 1979), and in *T. monteverdae* (100%) (COVILLE, 1982; BROCKMANN, 1992) was also observed in *T. antropovi* (80.5%). Nevertheless, REHNBERG (1987) observed that the preference (60%) of *T. politum* for juveniles occurred only at the beginning of summer and decreased to <5% at the end of the season. These observations indicate that the preference may change during the season.

The cocoon structure of the two species studied here was similar to that described for other species of the *albitarse* group (MATTHEWS & MATTHEWS, 1968; CROSS **et al.**, 1975; COVILLE, 1982; BROCKMANN & GRAFEN, 1989; BROCKMANN, 1992).

With respect to parasitoids, adult flies (Sarcophagidae) were observed emerging from nests of *T. politum* (CROSS **et al.**, 1975; BROCKMANN, 1980) and *T. monteverdae* (BROCKMANN, 1992), but not from the nests of *T. antropovi* and *T. aestivale*. In contrast, individuals of the chalcidids, observed emerging from nests of *T. antropovi* and not from nests of species of the *albitarse* group.

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